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REPLICATION OF SUBSTRATE DETAIL BY BARNACLES AND SOME OTHER MARINE ORGANISMS

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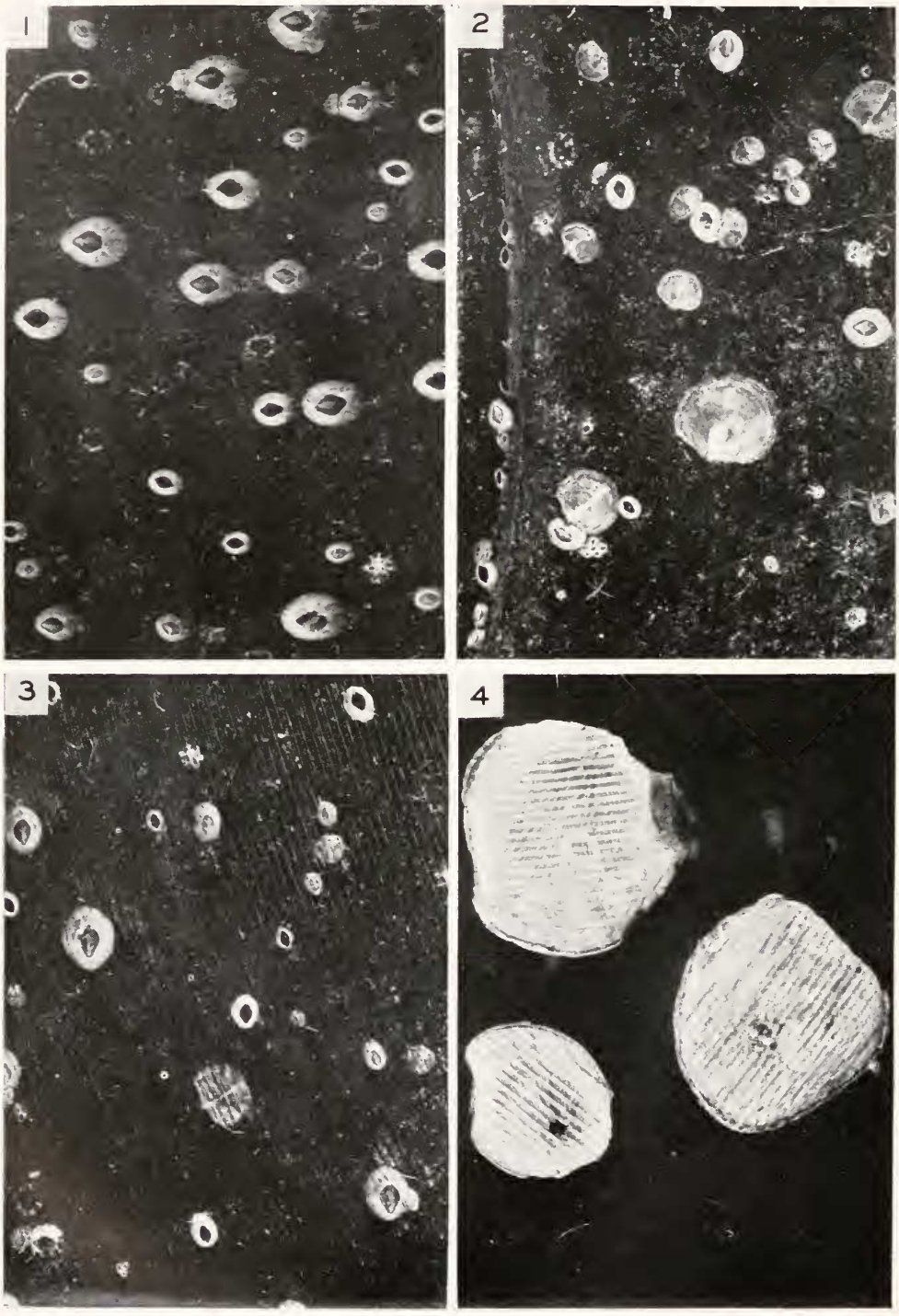
Many marine organisms exist for a short time as free swimming larvae before attaching themselves to a suitable surface and entering a new phase of their life cycle as sedentary individuals. Among these organisms are the acorn barnacles and some species of molluscs. Pomerat and Weiss (1946) found that glass plates with various surface textures to which the cypris larvae of the barnacles *Balanus amphitrite niveus* Darwin and *Balanus improvisus* Darwin attach does not affect the frequency of successful attachments. However, the writer found that the nature of the surface affects the orientation of the long and short axes of *Balanus eburneus* Gould and the topography of the calcareous compartments of *Balanus eburneus* Gould and the shells of the mollusc *Ostrea virginica* Gmel. Furthermore it is evident that the basal plate of the barnacle is subject to variations in form and topography according to the surface upon which growth takes place.

In order to study orientation phenomena and variations in form, it was necessary to use a surface of attachment affording consistent irregularities and for this purpose ordinary phonograph records were well adapted.

The records were submerged in horizontal and vertical positions several feet beneath the lowest tide level in the Mississippi Sound at Bayou La Batre, Alabama, and at the U. S. Fish and Wildlife Service laboratory on Santa Rosa Sound at Pensacola, Florida. Barnacle and oyster larvae of the species mentioned were found to attach readily and in large numbers to the black surfaces of the records. The age and size of the organisms ultimately collected depended, of course, upon the length of time the records were allowed to remain in the sea. The earliest examination of the records was made following a fourteen-day period of submergence. Many of these barnacles were assumed to be twelve to fourteen days old with regard to sedentary life, as it is possible for very large numbers of barnacle larvae to become attached during the first forty-eight hours of the submergence of a surface (Pomerat and Reiner, 1942).

The grooved surface offered by the phonograph records influenced the orientation of the barnacles to the extent that on one record 443 barnacles of a sample population of 663 had grown with their long axes parallel to the grooves in the record while the remaining 220 grew at various other degrees from parallel (Fig. 1). The 95 per cent confidence interval for this sample indicates that of the total number of barnacles attaching to the record, some 63 per cent to 71 per cent orient themselves

PLATE I



parallel to the grooves while not more than 37 per cent orient themselves at degrees other than parallel. The barnacles attached to the smooth surfaces of the records used as controls were oriented at random (Figs. 2 and 5). This fact tends to eliminate the possibility that geotropic or phototropic factors are greatly involved in the orientation of cypris larvae parallel with the grooves of the record. The oysters whether on the smooth or the grooved surface of a record did not show any tendency to become oriented and were attached at random (Figs. 2 and 3).

The external surfaces of the calcareous compartments of the barnacles were found to have duplicated the grooved pattern of the record while the basal plates which were in immediate contact with the record were found to have become ridged in a pattern similar to that of the record (Figs. 3, 4, 6, 7, 8). The grooves were of approximately the same width and depth and were continuous with those of the record. The grooves which appear on the compartments of the barnacle persist during subsequent growth although they were inclined to the right or left with respect to the grooves in the record with which they were continuous (Fig. 8). This shifting in space laterally occurs because of the movements of the individual compartments in the course of growth. The grooving of the record was not found to have affected the internal surfaces of the basal plate or the compartments of the barnacle. The terga and scuta were not affected in any way either externally or internally.

The ratio between length and width of *Balanus eburneus* Gould in many instances was affected by the presence of the grooves of the record and in consequence the shape of the barnacle was changed during growth. Regardless of the orientation the particular compartments and the parts of the basal plate of the barnacle that had to continue growth in a direction perpendicular to the grooves in the record were retarded in the rate of increase in length or width in the plane of attachment (Fig. 7).

This grooved and ridged condition was also found on the external and internal surfaces of both shells of the oyster, the grooved pattern of which was located on the external upper shell and the ridged pattern of which was located on the surface of the shell in contact with the record (Fig. 3). The grooves and ridges were well defined in the young oyster over the entire upper and lower shells both internally and externally, but they became somewhat obliterated after several months of age except at the extreme growing edges.

Other species of barnacles *Balanus improvisus* Darwin and *Balanus amphitrite niveus* Darwin were investigated by the use of phonograph records by Dr. C. M.

Explanation of the Figures

A comparison of living barnacles and oysters growing on the grooved and smooth surfaces of phonograph records. All barnacles and oysters are of the species *Balanus eburneus* Gould and *Ostrea virginica* Gmel., respectively.

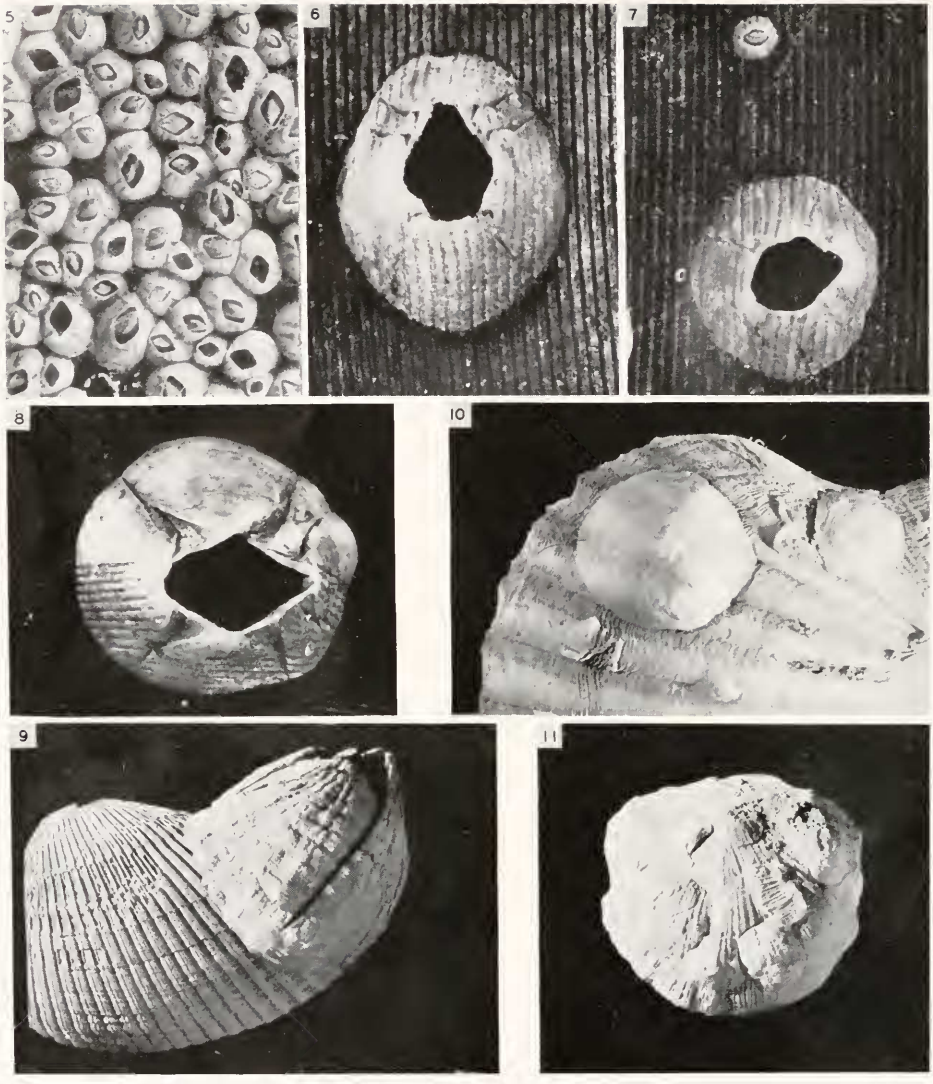
1. Orientation of the long axes of the barnacles parallel with the grooves of the phonograph record. (×4)

2. Random orientation of barnacles and oysters on the smooth surface of the record. Note that several barnacles are oriented along the groove at the left edge of the figure. (×4)

3. Random orientation of the oysters with the grooves of the record and showing grooves on the upper shell of the oyster (lower middle of figure) and grooves on the barnacles. (×4)

4. Several barnacles removed from the phonograph record showing the acquired ridging on their basal plates. (×4)

PLATE II



EXPLANATION OF THE FIGURES

A further comparison of living barnacles growing on phonograph records, a fossil barnacle, a living mollusc, and a fossil brachiopod attached to various substrates.

5. Random orientation of *Balanus eburneus* Gould growing on the smooth surface of a record. (× 4)

6. Grooving on the compartments of the barnacle *Balanus eburneus* Gould which are continuous with the grooves in the record. (× 12)

7. Two barnacles (*Balanus eburneus* Gould) growing with their long axes perpendicular to the grooves of the record showing a marked departure from the normal length-width ratio and showing grooving of the compartments. (× 12)

Pomerat (personal communication). These species, however, failed to show any such striation of the compartments. This would suggest a different pattern of calcium deposition in compartment formation.

Pilsbry (1916) found that the living barnacles, *Balanus rostratus apertus* Pilsbry and *Balanus balanus* Linnaeus, when growing on *Pecten* were capable of reproducing the ribs of the scallop's shell on its own compartments.

Darwin (1854) offered an explanation for the fact that the shape of sessile barnacles depended on their position and grouping while the surface of attachment has a great effect on that of the shell. As the walls are added to at their bases, every portion has at one time been in close contact with the supporting surface and, therefore, a strongly ribbed species such as *Balanus porcatus* DaCosta might closely resemble a nearly smooth species such as *Balanus crenatus* Bruguière. However, both were found to have a peculiar appearance owing to their attachment to a species of *Pecten*. Furthermore specimens of *Balanus patellaris* Spengler have been found which were curiously pitted like the wood to which they had adhered.

Among the fossil forms which exhibit similar phenomena is the barnacle *Balanus concavus* Bronn from the Miocene found attached to a ribbed mollusc from which it had obtained a ridged surface (Fig. 9). Pilsbry (1930) found that the compartments of the fossil barnacle *Balanus shilohensis* (Pilsbry) of the Miocene were smooth except when adventitiously sculptured by growth on a ribbed shell or other rough support.

A mollusc, *Anomia simplex* d'Orb, which was found growing on a ridged *Pecten* shell, exhibited the persistence of acquired ridging and grooving on its own shell (Fig. 10).

Hall (1870) found that the surface of the valve of the brachiopod *Crania scabiosa* (Hall) [*Petrocrania scabiosa* (Hall)] was sometimes obscured by the roughness of the substance to which it is attached and caused irregular growth by which it often assumed the features of the foreign body. Figure 11 shows the resulting irregularities of an Upper Ordovician *Petrocrania scabiosa* (Hall) when growing on the shell of *Rafinesquina ponderosa* Hall. The fossil brachiopod *Crania socialis* Hall [*Petrocrania scabiosa* (Hall)] was also reported by Hall (1892) to have maintained the marks of the sutures between the segments of a crinoid to which it was attached. Among the Pelecypods attachment by cementation has been found to result in a strongly vesicular structure in the attached shell. That this phenomenon may be a more general rule is emphasized by certain attached annelidan tubes such as *Cornulites proprius* Hall. Furthermore marked vesiculation of the shell has been found among brachiopods such as *Petrocrania* and *Richthofenia*, which are attached by a considerable surface of the shell (Hall, 1892).

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8. The barnacle, *Balanus eburneus* Gould growing both on the grooved and the smooth surface of the record. Note the angle of the grooves on the compartments with respect to the surface of the record. (× 8)

9. The fossil barnacle *Balanus concavus* Bronn attached to a *Pecten* showing grooving on its own compartments. (× 1.5)

10. The living mollusc *Anomia simplex* d'Orb attached to a *Pecten* showing grooving on its own shell. (× 2.5)

11. The fossil brachiopod *Crania scabiosa* (Hall) [*Petrocrania scabiosa* (Hall)] showing the acquired ridging derived from the shell of *Rafinesquina ponderosa* Hall. (× 1.5)

Kozlowski (1929) found that the fossil brachiopod *Philhedra mimetica* Kozlowski growing on the shell of *Camarotocchia* (*Wilsonia*) *tarda* (Barrande) reproduces the ridges. In addition the fossil brachiopod *Philhedra crenistriata* (Hall) was found capable of reproducing the substrate upon its own shell.

Discussion

The tendency for larvae of the barnacle *Balanus eburneus* Gould to become oriented with their long axes parallel with the grooved surface offered by the phonograph record was regarded as having occurred at the initial attachment when the cypris larvae were of an elliptical shape. Although the barnacles exercise slight movements in becoming firmly attached immediately following metamorphosis from the cyprid stage to the adult, the majority of them maintain their original position. It is quite possible that because of the elongate shape of the barnacle cyprid it more easily attaches itself parallel to the grooves than in other positions. The fact that oyster larvae are more or less radially symmetrical would seem to eliminate any possibility other than random chance of establishing their body axes in a particular direction when attaching to a phonograph record.

It is well known that the increase in length of the individual compartments of the barnacle is due to the secretion of building material from the lower edges of the valves (Darwin, 1854) and at the outer edges of the basal plate. This is substantiated by the fact that the grooves on the barnacle persist to the upper edges of the compartments. The secretion of the shell building material onto the grooved substrate leaves no other course for the building material than to arrange itself to conform with the pattern offered by the substrate. With subsequent secretions the building material is arranged similarly and eventually a continuous groove or ridge appears.

The oyster also became grooved and ridged while growing on phonograph records, as did an *Anomia simplex* d'Orb when attached to *Pecten* due to the fact that the mantle secreted the building material onto the available substrate and the material was obliged to follow the contours of the surface. In these two molluscs the lower shells reproduce the characteristics offered by the substrate and, therefore, the upper shells conform to the pattern conceived by the lower shells.

There are variations in the normal length-width ratio of many barnacles growing on a grooved surface. This may be attributed to the following fact. In order for the compartments and the parts of the basal plate of the barnacle growing perpendicular to the grooves in the record to attain the same linear proportions at the same rate as would its partner on a plain surface, a greater total surface area must be covered by the shell building material and in consequence a greater amount of time and material is required.

While all species of barnacles adhere closely to the substratum, not all barnacles reproduce the pattern of the substrate upon which they grow. It would seem that the species which do so may gain some selective advantage by the mechanical mimicking of a substrate pattern upon their compartments. This duplicating phenomenon is probably not merely a consequence of gaining an adequate fixation to the surface.

Summary

1. Barnacles of the species *Balanus eburneus* Gould were found to orient themselves with their long axes parallel to the grooves in the substrate, while oysters (*Ostrea virginica* Gmel.) were found to orient themselves at random.

2. The grooving in the substrate was found to affect the topography of the compartments and the basal plate of the barnacle *Balanus eburneus* Gould. The grooves are duplicated upon the compartments and the ridges upon the basal plate. Any one groove on the record causes a ridge to occur on the basal plate and a groove to appear on the compartments of the barnacle. These grooves and ridges are initiated at the early growth stages and persist irrespective of the ultimate size of the organism.

3. In a similar manner the grooved surface of the phonograph records affects the shells of the mollusc *Ostrea virginica* Gmel. both externally and internally by causing grooves and ridges to appear on the upper and lower shells.

4. The living species of barnacles, *Balanus rostratus apertus* Pilsbry, *Balanus balanus Linnaeus* (Pilsbry, 1916), *Balanus porcatus* DaCosta, *Balanus crenatus* Bruguière, *Balanus patellaris* Spengler (Darwin, 1854), and the fossil barnacles *Balanus shilohensis* (Pilsbry) (Pilsbry, 1930) and *Balanus concavus* Bronn also have their compartments affected by the substrate to which they attach.

5. The mollusc *Anomia simplex* d'Orb may also exhibit characteristics of the surface to which it attaches.

6. The fossil brachiopods *Crania scabiosa* (Hall) [*Petrocrania scabiosa* (Hall)] (Hall, 1870), *Philhedra mimetica* Kozlowski (Kozlowski, 1929), *Philhedra crenistriata* (Hall) and the annelid tube of *Cornulites proprius* Hall (Hall, 1892) have been found to assume certain features of the substrate upon which they grew.

7. Grooving and ridging occur on the barnacle *Balanus eburneus* Gould because the shell building material secreted by the organism in maintaining close contact with the substrate is obliged to follow the contours of the surface. This close association during growth eventually leads to the formation of grooving on the compartments and ridging on the basal plate.

8. A similar explanation for the fact that young of the molluscs *Ostrea virginica* Gmel. and *Anomia simplex* d'Orb show ridging and grooving phenomena is offered, with the exception that the lower shell of a mollusc acts as the pattern to which the upper shell must conform during growth. This explanation is probably adequate for similar substrate reproduction by the brachiopods.

9. Variations in the normal length-width ratio of *Balanus eburneus* Gould result from growth upon a grooved surface. This was attributed to the fact that the compartments and the parts of the basal plate which must grow perpendicular to the grooves are retarded in the rate of increase in length or width in the plane of attachment.

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